Paulo Jodevi

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20. F. G. Brieger

PHYLOGENIE AND EVOLUTIONARY THEORY

Of the numerous aspects of the problem of evolutionary changes, one has almost completely absorbed the general interest of geneticists during the last 50 years: that of speciation. Though from certain points of view, especially from that of the experimental geneticist, the species requires a special interest, it is my intention, in the present comunication, to try to show, that nearly all features of the evolution of all taxa are of the same nature, and that there is no necessity of considering species formation as something special, nor that there is any need for distiguishing between micro-macro- or mega-evolution.

One fact, which Linné already discovered and used, though without stating it clearly, is that — when comparing a large number of specimens for certain characters — it becomes evident that variation is discontinuous, and thus groups or clusters of elements are clearly separated from others. Next, when one uses subsequently more and more caracters, starting with those of a more general distribution, it becones furthermore evident that each large cluster may be subdivided progressively into smaller and smaller units. Thus there are two set of facts: the discontinuous nature of variation and the hierarchical subordination of smaller and smaller clusters. On the other hand, wich of the levels of distinction and how many of them one chooses as "taxon" denominated by a latin name, it is as arbitrary as the coordination of such level in different series. Thus within the family I am most familiar with, the orchids, the subfamily **Cypripedioideae** contains only four major clusters of elements, which might call genera, monotypic subtribes or tribes, while in the **Epidendroideae** and **Oncidioideae**, with several hundred genera, a number of taxonomic units can be identified between what is called subfamily and the genus. The origin of discontinuous variation can be easily explained by the current theory of evolution, i. e. by the interplay of mutations without direction and the directing force of selection, but this theory cannot explain the hierarchical subordination of taxa within each phylogenetic series. Here we must assume that, after an evolutionary diversification has been going on for some time, a mechanisme of phylogenetic fixation sets in which excludes any further change of a given character. The genetic mechanism of this phylogenetic fixation can be explained, as I have stated elsewhere, by the following argument, somewhat analogous to Fisher's theory of the origin of the dominance. He postulated that selection favoring some allele of a given locus, will in turn give preference to such alleles which give the favored phenotypic expression and at the same time will suppress, in heterozygotes, the manifestation of any other mutant. Such other mutation continues to occur, but their manifestation is restricted to the homozygous stage. Phylogenetic fixation consists in the evolution of a complex of epistatic inhibitors, which suppress the manifestation of any mutants with a different phenotype than the one which corresponds to the selective trend in action. Such a fixation process is not necessarily irreversible. Some new mutations may permitt a new selective trend or the external conditions may cause a change in the selective trend, and thus put out of action the gene complex of phylogenetic fixation. However such reversals must be rare in nature, and the general occurence of distinct large taxonomic units shows how constant, in general, phylogenetical fixation must be.

The generally occuring hierarquical subordination of taxa shows furthemore, that fixation of different characters is not a continous process, but occurs in jumps, in the sense that one character complex becomes fixed after the other. This time sequence may sometimes be incomplete, and some characters may undergo evolutionary diversification and fixation nearly simultaneously, causing complex situations for the taxonomist. Thus in the two large groups of higher orchids two processes of diversification took place: a change from terminal to lateral inflorescence and the formation of the content of pollen sacs, or the formation of complex pollinaria ,by the addition of a strip of stylar tissue, the stipes, to the pollinium. About 45% of the taxons each show either terminal inflorescence and simple pollinia or lateral inflorescences and complex pollinaria, but there are an aditional 5% each for the alternative possibilities of caracter combination. Thus we must assume that here diversification and phylogenetical fixation occured to some extent simultaneously. There is also no orderlines in the sequence of this fixation. Thus, for instance in orchids, the genus **Encyclia** shows extreme constancy of vegetative characters, while the related genus **Epidendrum** contains a very wide range of variation of these organs. Flowering time, one of the main isolating mechanism in orchids, is different in nearly all species of **Laelia** or **Cattleya,** while it is nearly constant for all species of **Schomburgkia,** when grown under identical conditions. Thus one cannot consider any character as more important, because it became phylogenetically fixed before another one. A very early fixation within a phylogenetical series, for instance at a high level considered as family or a higher order still, does not mean that their distinctive characters are more "essencial", but only that they are common to a larger number of lower taxa. Since there is no objective criterium for considering character as more essencial or more fundamental, one gets only subjectively the impression that this is the case, simply because the character is in common to a very large number of lower taxa. This argument leads to the conclusion, that there is really no necessity of distinguishing degrees of evolution, as different by nature, such as micro-, macro- or mega-evolution, the only difference being of the time of phylogenetic fixation in an evolutionary series.

In the majority of taxonomic species this definition will be satisfactory, but a certain number of cases will remain some doubts as to what represents this ultimate category, and one consider necessary to add still some infraspecific categories, such as subspecies, also with a constant discontinuity of variation between subspecies, though referring to characters which in comparison with differences between species may seem of less serious nature, an evidently subjective judgement. If one may consider as initial stages of species formation, varieties showing not very constant differences or cryptospecies which implicitely present conditions for constancy though distinguishing characters are absent, is a difficult question, since nobody can foresee the future course of evolution.

In the same way, as selection acts mainly as a negative factor, eliminating all character manifestations except those favored by the selective trend, phylogenetical fixation is a factor which reduces in a general way the possibilities of evolutionary variation. This may explain why in most phylogenetical series certain evolutionary changes are excluded, so that the reduced number of remaining possibilities gives the impression of the existance of "evolutionary tendencies" or of "orthogenetic trends". The elimination of the possibility of some evolutionary changes, may result in leaving for further evolution such a restricted number of possibilites that the relative frequency of parallel evolution in different branches of one phylogenetical series become frequent.

From the view point followed so far, one must conclude that the species does not represent any special taxonomic category, but only the lowest category, where still groups of specimens can be distinguised from others, owing to a constant discontinuity of some characters. Thus I accept the definition of the species concept of the taxonomist, requiring distinctiveness of some characters and constancy within a given time limit, and the latter requirement includes the existance of efficient isolating mechanismes.

The species representing the lowest existing member in a phylogenetical series, is thus characterized by a maximum of already fixed and thus constant characters and correspondingly with a minimum of still variable ones. This however is correct only for a given moment in the evolutionary process, and probably the number of cases, where the species is the end product of a phylogenetical series, which has exhausted all evolutionary possibilities and has become totally fixed, will be very rare. Some data in our work on orchids shows this point very clearly. Owing to their excceedingly smallness and ligth weight, orchid seeds can be distributed widely and thus become dispersal even from one tropical continent to another one.

Of near than a thousand African species belonging to subtribes or genera, which occur predominantly in tropical America or Africa, and which thus represent dispersed elements, only 2 are common to both Africa and America and 4 to Africa and South-East-Asia. All the others are different from those in the original area. Equally there are a number of genera in the African tropic which must have evolved after intercontinental dispersal. Intercontinental dispersal is however a relatively rare event, and thus the majority of dispersals should have occured long ago and more recent ones should be rare. The relative frequency of intracontinental dispersal, from the Andean region to South- and East-Brazil is much higher, and thus more recent cases must also be more frequent. In fact, it has been possible to observe a whole series of cases with gradual changes, from dispersed species without any change, to others with the formation of pairs of subspecies or species, showing that the species, both in the original and the new area constantly, though slowly changing, without necessarily splitting up into more than one new species. Thus number of cases where a kind af explosive evolution has occured and groups of nearly related species formed, frequently at least some of them fully sympatric evolve are much rare, and several of these cases are now under closer examination.

These latter cases show another features which seems to be common to taxa of any level: the disparity of evolutionary activity between taxa of the same level. The majority of the orchid species are isolated ones within their genus and in a way equidistant from other species. Only exceptionally clusters of very nearly related species can be identified. Among the next higher level, the genera, about 80% of the genera totalling around 750, are small, containing only up to 15 species, 18% are large genera with up to 150 species and only about 2% are very large genera with up to 1.000 species. The latter show that they are characterized by a high evolutionary activity, since they contribute proportionally more to the formation of new species after the dispersal to another continent than the other two categories. On the other hand, the smaller genera, and in the the same way the isolated species, may represent either taxa which have not yet reached an explosive stage, which have passed already beyond it and suffer progressive elimination or may be groups with low evolutionary activity.

It has been my intention to show that from a general phylogenetical point of view, the species does not show any difference from that of any other taxon, and furthermore that in addition to mutations and selection, phylogenetic fixation is an important feature of the evolutionary process.